Supplementary Material
Power of the wingbeat: modelling the effects of flapping wings in vertebrate flight

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S1 Profile drag polar

Several studies have aimed at measuring the drag polar of birds [1, 2, 3, 4], bats [5] or their wings [6, 7, 8]. However, these studies generally measure the total drag polar, including body drag (for free flying birds) and induced drag. Body drag can be easily subtracted, but induced drag is difficult to measure. Tucker and Heine 1990 [4] measured the drag polars (for varying wing configurations) of a Harris' hawk (*Parbuteo unicinctus*). They subtracted body drag and an estimated induced drag with an induced drag factor of 1.1. Figure S1 shows the resulting profile drag measures together with the profile drag model that we used for our computations, i.e. $C_{D\mathrm{v},0} + C_{D\mathrm{v},2}C_L^2$ with $C_{D\mathrm{v},0} = 2.66/\sqrt{Re}$ and $C_{D\mathrm{v},2} = 0.03$.

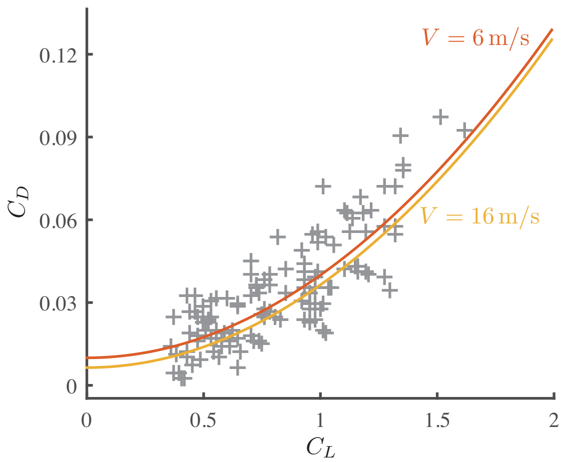

Figure S1: Profile drag polar used in the model for $C_{D\mathrm{v},2} = 0.03$ compared to profile drag measurements from a Harris' hawk (data points measured from [4, fig. 5]).

S2 Sensitivity of lift dependent profile drag/power

The solution for lift dependent profile power depends on the value of $C_{D\mathrm{v},2}$ and the chord length c:

$$\mathbf{K}_{\mathrm{vis}} = \mathbf{K}_{\mathrm{ind}} + 4C_{D\mathrm{v},2}\ \mathrm{diag}\left(\frac{A_j}{c_j}\right),$$

in

$$P_{\mathrm{v},2} = \frac{1}{2}\rho f \mathbf{\Gamma}_{\mathrm{vis}}^T \mathbf{K}_{\mathrm{vis}} \mathbf{\Gamma}_{\mathrm{vis}} - \frac{1}{2}\rho f \mathbf{\Gamma}_{\mathrm{ind}}^T \mathbf{K}_{\mathrm{ind}} \mathbf{\Gamma}_{\mathrm{ind}}.$$

With bird and bat species having different aspect ratios ($AR \propto 1/c$), this means that the factors $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$ are not entirely species independent. Also, when future experiments provide more accurate estimates, the value of $C_{D\mathrm{v},2}$ might need to be adjusted. In the above equation AR and $C_{D\mathrm{v},2}$ mathematically have

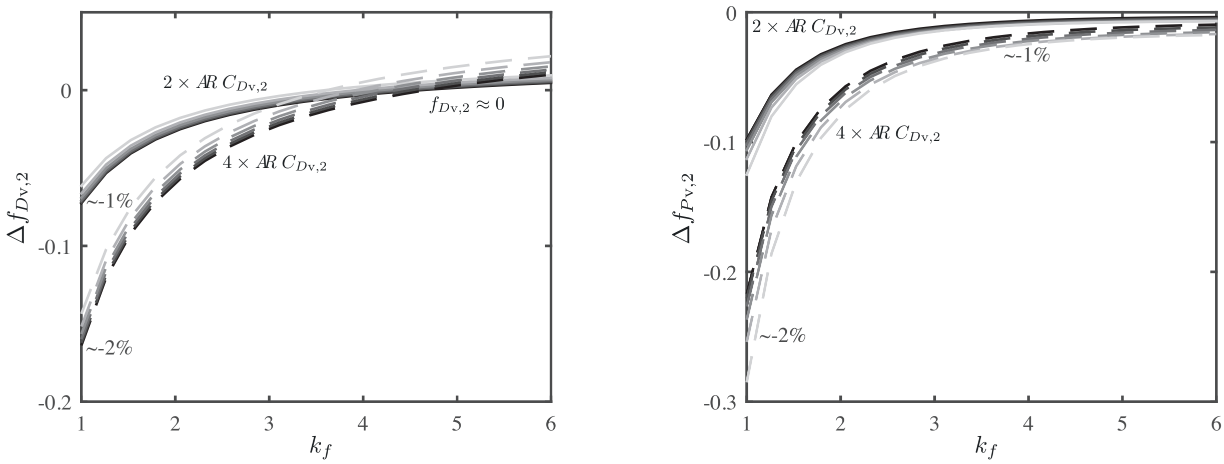

Figure S2: Effect of doubling (solid lines) and quadrupling (dashed lines) $AR\, C_{D\mathrm{v},2}$ on $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$. Dark shaded lines for stroke-plane $\varphi = 0°$ and light shaded lines $\varphi = 50°$. Percentages indicate the local relative difference to the original values.

the same effect. To test the sensitivity of $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$ we have repeated the computations for different values of the product $AR \cdot C_{D\mathrm{v},2}$. Table S1 shows how the fitted coefficients of $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$ are affected. For the fitting procedure we used the weights from the original data set, to ensure that only the lift dependent profile drag/power are affected. The largest difference occurs for $f_{D\mathrm{v},2}$ coefficient $p_{1,0}$ which itself is rather small. Figure S2 shows the absolute difference in $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$ compared to the original combination $AR \cdot C_{D\mathrm{v},2}$. The largest difference is found for $f_{P\mathrm{v},2}$ at very low reduced frequencies: $\Delta f_{P\mathrm{v},2} \approx -0.25$, which relative to the value of $f_{P\mathrm{v},2}$ is only a 2% decrease. For $f_{D\mathrm{v},2}$ the relative effect at higher reduced frequencies is very large, due to the fact that the absolute value goes through zero.

Considering that

$$\frac{P_{\mathrm{v},2}}{P'_{\mathrm{v},2}} = 1 + f_{P\mathrm{v},2}\frac{T}{L} + \Delta f_{P\mathrm{v},2}\frac{T}{L},$$

it follows that the differences shown in figure S2 are multiplied with the thrust ratio, which is of the order 1/10, so that a difference $\Delta f_{P\mathrm{v},2}$ of order 1/10 would amount to a difference in flapping power of 1% of the non-flapping power. We therefore conclude that the model is relatively insensitive to changes in AR and $C_{D\mathrm{v},2}$.

Table S1: Coefficients of $f_{D\mathrm{v},2}$ and $f_{P\mathrm{v},2}$ for different values of $AR \cdot C_{D\mathrm{v},2}$. First column is showing the original result and the second and third columns indicate the relative difference to the original by doubling and quadrupling $AR \cdot C_{D\mathrm{v},2}$ respectively.

$AR \cdot C_{D\mathrm{v},2}$		original	2×	4×
		0.183	0.366	0.732
$f_{D\mathrm{v},2}$	$p_{0,0}$	9.298	-1.0%	-2.2%
	$p_{0,2}$	1.301	+0.4%	+0.6%
	$p_{1,0}$	-0.659	-3.1%	-6.8%
	$p_{1,1}$	-1.521	-0.2%	-0.6%
$f_{P\mathrm{v},2}$	$p_{0,0}$	8.851	-1.0%	-2.3%
	$p_{0,2}$	2.807	-0.5%	-1.3%
	$p_{1,0}$	1.354	-0.6%	-1.3%
	$p_{1,1}$	-0.943	0.6%	1.4%
	r	1.201	-0.7%	-1.4%

S3 Observed flight speeds jackdaw (*Corvus monedula*)

We analysed 30 tracks of (flocks of) jackdaws in powered flight recorded using an ornithodolite, which is a laser range finder combined with an anemometer [9]. The observations were weighted using the standard error on the true airspeed ($w = \sqrt{N/\sigma^2_{\text{Trueairspeed}}}$), $\sigma^2_{\text{Trueairspeed}}$ being the variance on the measured mean flight speed for a track and N the number of observations for that track. There was a significant effect of vertical speed, wind speed (difference between groundspeed and airspeed Vg-Va) and of flock size (ln (Flocksize)). With a confidence level of 95% the expected average speed is between 11.6 m/s and 14.3 m/s for a single bird in horizontal flight without wind.

For the jackdaw that is used as an example in the current work, the maximum range speed based on aerodynamic power is estimated to be 12.1 m/s by the model presented in this work, while it is predicted to be 15.9 m/s by the Pennycuick model. Based on metabolic rate, using the same energy conversion for both models, the estimates increase to 12.5 m/s and 16.7 m/s, respectively.

Table S2: Summary statistics jackdaw flight speeds

Linear regression model:				
	Trueairspeed ~ 1 + Verticalspeed + (Vg-Va) + ln(Flocksize)			
Estimated Coefficients:				
	Estimate	SE	tStat	pValue
(Intercept)	12.923	0.65987	19.584	≪0.0001
Verticalspeed	-1.7042	0.5683	-2.9988	0.0059033
(Vg-Va)	-0.30577	0.14256	-2.1448	0.041482
ln (Flocksize)	0.64795	0.25511	2.5398	0.017409
Number of observations: 30, Error degrees of freedom: 26				
Root Mean Squared Error: 2.74				
R-squared: 0.537, Adjusted R-Squared 0.484				
F-statistic vs. constant model: 10.1, p-value = 0.000142				

S4 Wing twist and lift coefficient

In the model we describe we do not include any limitations on the lift coefficient (i.e. wing stall) or the amount of spanwise twist of the wing that would be required to obtain that lift coefficient. This means it will always assume the ideal distribution of circulation. It may, however, occur that the wing is physically not able to produce this optimal distribution.

In the Hall and Hall model [10] the distribution of the required lift coefficient, along the span and throughout the wingbeat, can be estimated from the computed distribution of circulation (Γ), the local wing chord (c) and the effective local velocity (V)

$$C_\ell = \frac{2\Gamma}{Vc}.$$

For a rough estimate of the required wing twist, the lift coefficient may be related to a required angle of attack by assuming a lift slope for the local aerofoil. Here we used a slope of 5.7 rad^{-1} [11, Appendix D; NACA0006]. The wing twist is then found from

$$\theta = \frac{C_\ell}{5.7} + \alpha_{\mathrm{i}} - \alpha_{\mathrm{g}},$$

where α_{i} is the induced downwash angle and α_{g} the angle between the effective wing velocity and the flight path.

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